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Probing the photosynthetic efficiency of some European and Anatolian Scots pine populations under UV-B radiation using polyphasic chlorophyll *a* fluorescence transient

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Abstract

The study was carried out to examine the photosynthetic efficiency of Scot pine populations, originated from various European countries and Anatolia in Turkey, exposed to UV-B radiation. Seeds were germinated and grown in the nursery; three-year-old seedlings were exposed to UV-B for two days, eight hours per day. The photosynthetic efficiency was probed by chlorophyll *a* fluorescence at 24 h after UV-B treatment and analysed by JIP-test. UV-B caused reduction in quantum yields and electron transport at both donor and acceptor sides of photosystems. The performance indexes of seedlings were also negatively affected by the treatment. Populations from France, England, and three provenances of Turkey showed sensitive responses, while the populations from Spain, Romania, and Ilgaz performed their photosynthesis better. We found that UV-B affected at different levels the photosynthetic functionality of populations. Chlorophyll *a* fluorescence technique is very useful to identify the UV-B tolerance of different Scots pine populations, however, further studies based on molecular analyses should be applied to explain their evolutionary history.

Additional key words: photochemistry; photosynthetic performance; *Pinus sylvestris* L.; ultraviolet-B.

Introduction

Light is an energy source for photosynthetic and developmental processes of plants. Ultraviolet radiation (UV) is a fraction of the nonionizing region of solar spectrum. Generally, UV radiation is divided into three groups: UV-A (320–400 nm), UV-B (280–320 nm), and UV-C (100–280 nm) (Annan 2014, Björn 2015). The UV-A is relatively harmless, whereas UV-B has many direct and indirect damaging effects on living organisms and UV-C is lethal for many of life forms. The amount of UV-B reaching the Earth's surface has been increasing due to depletion of stratospheric ozone layer (Singh *et al*. 2008), while UV-C does not reach the surface and gets absorbed by the ozone layer. Additionally, an increase in stratospheric ozone layer has been observed in recent years, but the recovery of ozone layer has not provided a decrease in UV-B radiation at the Earth's surface yet (Bais *et al*. 2018). Although UV-B is a minor component of solar radiation, due to its high energy with the shortest wavelength of the solar spectrum reaching the atmosphere, elevated UV-B radiation can affect plant growth and metabolism (Caldwell *et al*. 1998, Huarancca Reyes *et al*. 2018). It has detrimental effects on main molecules of cells, such as proteins, lipids, nucleic acids, and photosynthetic pigments, thus, main processes of cells including photosynthesis are adversely affected or inhibited (Jansen *et al*. 1998, Dobrikova *et al*. 2013). It has been suggested that reduction in photosynthesis has been associated with damage of PSII, declines in pigment contents and Rubisco activity (Fiscus and Booker 1995, Jansen *et al*. 1998, Vass 2012). Plants have protective and repair mechanisms to UV-B, such as production of UV-B-absorbing compounds (mainly flavonoids and phenolic compounds), increase in the expression of genes

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Abbreviations: ABS – absorption; ABC/RC – absorption flux per reaction center; Area – total complimentary area between the fluorescence induction curve; ChlF – chlorophyll *a* fluorescence; CS – cross section; ET – electron transport; F_0, F_m – initial and maximum chlorophyll fluorescence intensity; JIP-test – analysis for the interpretation of OJIP transients; K-, J-, and I-step – intermediate steps in the ChlF rise appearing between F_0 and F_m at about 0.3, 2, and 30 ms, respectively; OEC – oxygen-evolving complex; OJIP – transient fluorescence induction defined by the names of its intermediate steps; PCA – principal component analysis; PI_{ABS}, PI_{TOTAL} – performance indexes; PQ – plastoquinone; RC – reaction center; TR_0 – trapped energy flux; UV-B – ultraviolet radiation B; ΔV_{IP} – relative amplitude of the I–P phase of Chl *a* fluorescence.
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involving in UV-B protection and repairing UV damage, activation of antioxidant defence system, and changes in plant structure. Therefore, responses of plants to UV-B may exhibit variations among species, even between different individuals of the same species. For instance, it has been found that barley cultivars showed different responses to UV-B (Hideg *et al*. 2006, Çakırlar *et al*. 2008). Jansen *et al*. (1998, 2004) stated that UV-B tolerance depends on the balance between damage reactions and both repair and regulation of the general stress tolerance pathways.

In photosynthetic organisms, light energy is absorbed by chlorophyll (Chl) within the light-harvesting complex (LHC) and can be dissipated *via* photochemistry, by heat, or as fluorescence (Murchie and Lawson 2013). Chl fluorescence measurements are widely used as a reliable and noninvasive tool to examine and evaluate the photosynthetic performances of stressed or nonstressed plants (Baker and Rosenqvist 2004, Oukarroum *et al*. 2007, Brestič and Živčák 2013, Goltsev *et al*. 2016, Stirbet *et al*. 2018). The yield of fluorescence emission, a measure of reemitted light from PSII, provides valuable information about the light energy utilization and/or the quantum efficiency of photochemistry and heat dissipation (Murchie and Lawson 2013, Oukarroum *et al*. 2018, Stirbet *et al*. 2018, and references therein). When dark-adapted photosynthetic samples are illuminated by saturated light, polyphasic fluorescence transients (OJIP transients) are observed and can be plotted on logarithmic time scale (Goltsev *et al*. 2016, Kalaji *et al*. 2018). The rise in the fluorescence transients (from F_0 to F_m) is associated with the reduction of electron carriers in the thylakoid membrane (Strasser *et al*. 2004, Lazár 2006, Kalaji *et al*. 2014). The shape of the OJIP curves under a variety of environmental conditions (or existence of any type of stress) could change regarding to photosynthetic efficiency of plants. The JIP-test was presented for analysis of the OJIP transients (Strasser and Strasser 1995) and it gives information related to structural and functional parameters that quantify the efficiency of photosynthetic apparatus as well as the functionality of PSII acceptor and donor sides (Yusuf *et al*. 2010, Goltsev *et al*. 2016, Kalaji *et al*. 2018). The O–J represents the reduction of the acceptor side of PSII (and also gives information on the connectivity between the PSII photosynthetic units), the J–I is associated with the partial reduction of the PQ pool, and the I–P reflects the reduction of the acceptor side of PSI (Yusuf *et al*. 2010, Ripoll *et al*. 2016). Many parameters could be calculated from obtained data and provide information about the PSII and PSI functionality. Photosynthetic activity measurements (especially Chl *a* fluorescence parameters) have been widely used to screen and reveal the effects of these environmental factors on photosynthetic behaviour of plants (*e.g.*, Strasser *et al*. 2010, Ceppi *et al*. 2012, Oukarroum *et al*. 2015, Dabrowski *et al*. 2016, Wijewardana *et al*. 2016, Çiçek *et al*. 2018, Kalaji *et al*. 2018, Baba *et al*. 2019). It has been reported that UV-B leads to downregulation of photosynthesis of *Arabidopsis thaliana* (Coffey and Jansen 2019, Khudyakova *et al*. 2019, Schultze and Bilger 2019), blueberry (González-Villagra *et al*. 2020), grapevine (Doupis *et al*. 2016), sugar beet (Rahimzadeh Karvansara and Razavi 2019), and soybean (Choudhary and Agrawal 2015).

The Scots pine (*Pinus sylvestris* L.), adapted to the annual cycle of radiation and temperature in the northern climate (Kim *et al*. 2018), is a medium-sized conifer, and also has high ecological and economic value. Scots pine is one of the most abundant tree species in Europe and northern Asia (Juntunen *et al*. 2002, Houston Durrant *et al*. 2016, Kim *et al*. 2018), and it exhibits a distribution range from Spain to the far east of Russia (Houston Durrant *et al*. 2016). It can grow at the wide range of latitudes (from northern Scandinavia to southern Spain) and elevations (from sea level to altitudes over 2,500 m) (Sinclair *et al*. 1999, Houston Durrant *et al*. 2016). Environmental factors including drought, salinity, heat, UV-B radiation, *etc.* influence the growth, development, and distribution of plants involving trees such as Scots pines. There are limited studies in the literature related to the effects of UV-B radiation on the photosynthetic apparatus response of Scots pine populations. Moreover, there is a lack of such studies sampling a large scale of its distribution (from Spain to England and Turkey). Therefore, the objective of this study was to evaluate the photochemical efficiency, probed by Chl fluorescence measurements, of ten Scots pines (*Pinus sylvestris* L.) subjected to enhanced UV-B radiation originated from various European countries and Turkey. In addition, photosynthetic efficiency of the Turkish populations was examined for the first time. In our study, we found that France (FR) and Sarıkamış (TRS) populations were adversely affected by UV-B more than other populations, whereas Spain (SP) and Ilgaz (TRI) populations exhibited better photosynthetic performance under UV-B.

Materials and methods

Plant material: Ten Scot pine (*Pinus sylvestris* L.) seedlings originated from Spain to UK and Anatolia, were used in the present study. Three-year-old seedlings were supplied from the greenhouse garden of the Central Anatolian Research Directorate of Republic of Turkey Ministry of Agriculture and Forestry. The list of main features of Scots pine populations (country of origin and geographical features) are following (*see* text table below). Experiments were performed in a controlled growth room at 25 ± 1°C with a 16-h photoperiod at 40 ± 5% humidity and light intensity of 250 μmol(photon) m^{-2} s^{-1}, which was provided by cool white fluorescent light.

UV-B treatment: Three-year-old Scots pine seedlings were separated into two groups: control and treated. The control group was not irradiated with UV-B and kept at the growth room which was described above. The treated group was irradiated with narrow-band UV-B (spectral peak at 306 nm) fluorescent tubes (*G15T8E*, *USHIO*) 2 d for 8 h per day (UVBBE 2.88 kJ m^{-2} per d). A 30-cm distance between the top of the seedlings and UV-B lamp was kept constant. UV-B treatment was applied alone in dark. Following the UV-B application for 8 h, the seedlings were transferred to controlled growth conditions described above. Chl fluo-

Country	Population	Code	Altitude [m]	Latitude	Longitude
Spain	Sierra Nevada	SP	1,700	37°00'N	3°30'W
Turkey	Kayseri-Pınarbaşı	TRP	1,840	38°43'N	36°13'E
Turkey	Çatacık-Değirmendere	TRC	1,550	39°58'N	31°07'E
Turkey	Sarıkamış-Sarıkamış	TRS	2,350	40°18'N	42°37'E
Turkey	Ilgaz-Yenice	TRI	1,500	41°01'N	33°49'E
Turkey	Vezirköprü-Kunduz	TRV	1,200	41°09'N	35°01'E
France	Mont Ventoux	FR	1,121	44°10'N	05°13'E
Romania	Brasov Mountains	RO	550	46°01'N	25°14'E
Germany	Waldsieversdorf	D	75	52°32'N	14°03'E
England	psySTN4-01SI	UK	360	57°12'N	3°37'W

rescence measurements were made 24 h after the UV-B treatment.

Polyphasic Chl *a* fluorescence measurements: To understand the UV-B effects on the photochemical efficiency of Scots pine populations, Chl *a* fluorescence measurements were performed using *Handy-PEA* fluorimeter (*Plant Efficiency Analyser*, *Hansatech Instruments Ltd*., King's Lynn, UK). Dark-adapted needles (for 30 min) were illuminated homogeneously over an area of 4 mm in diameter with an array of three light emitting diodes (LED) providing a pulse of saturating light intensity of 3,000 µmol(photon) m^{-2} s^{-1}. Data, recorded between 50 µs and 1 s, were used to calculate some JIP-test parameters. JIP-test is based on a proposed theory of energy fluxes in biomembranes (Strasser *et al*. 2000) and can be utilized to screen many photosynthetic samples rapidly and to provide information about the structure and function of their photosynthetic apparatus (Strasser and Strasser 1995). Selected JIP-test parameters used in this study were calculated from obtained data: (*1*) Efficiencies and quantum yields; *i.e.*, maximum quantum yield of primary PSII photochemistry (F_v/F_m), efficiency with which a PSII trapped electron is transferred from Q_A^- to PQ (Ψ_0), quantum yield for electron transport (φ_{E0}), the quantum yield for the reduction of PSI end electron acceptors per photon absorbed (φ_{R0}), and efficiency with which an electron from the intersystem electron carriers is transferred to end PSI acceptors (δ_{R0}). (*2*) Specific fluxes; *i.e.*, the absorption/antenna size (ABS/RC), maximum trapping (TR_0/RC), electrons transferred (ET_0/RC), and dissipated (DI_0/RC) per active PSII. (*3*) Phenomenological energy fluxes; *i.e.*, the absorption (ABS/CS_0), maximum trapping (TR_0/CS_0), electron fluxes transferred (ET_0/CS_0), dissipation (DI_0/CS_0) and amount of active PSII RCs (RC/CS_0) per cross section. (*4*) The most sensitive JIP parameters, performance indexes (PI_{ABS} and PI_{TOTAL}) (Strasser *et al*. 2004, 2010). In addition, some JIP parameters give information about the PSII donor side; *i.e.*, inactivation and probable damage of the OEC (V_K/V_J) (Ripoll *et al*. 2016), acceptor side of PSI (with ΔV_{IP}) (Ceppi *et al*. 2012), the proportional pool size of electron acceptors in PSII and the indicator of PSII structure and functioning [Area and $SFI_{(abs)}$, respectively]. Equations for calculation of JIP-test parameters are also given in Appendix.

Statistical analysis: Analysis of variance (*ANOVA*) of the data with three replicates (n = 10) was performed using *SPSS 20.0* software (*IBM SPSS Statistics*) and the significance of differences between treatments and populations was compared using LSD test at p<0.05. Additionally, Principal Component Analysis (PCA) was carried out to discriminate the populations using *R*.

Results

The significant change in Chl fluorescence transient (OJIP) curve of Scots pines subjected to UV-B was determined. UV-B treated seedlings exhibited much slower fluorescence rise, and much lower I–P amplitude as compared to control seedlings, which exhibited a typical OJIP curve (Fig. 1).

UV-B radiation significantly decreased the photosynthetic performance indexes (PI_{TOTAL} and PI_{ABS}) of all Scots pine populations indicating changes in structural properties and functioning of PSII and PSI (Fig. 2). The highest decreases in PI_{TOTAL} were observed in France (FR), Çatacık (TRC), and Sarıkamış (TRS) populations, whereas the lowest decreases were found in Spain (SP), Romania (RO), and Ilgaz (TRI) populations. All components of PI_{TOTAL} parameter, *i.e.*, PI_{ABS}, $\Psi_0/(1-\Psi_0)$, $\varphi_{P0}/(1-\varphi_{P0})$, $\delta_{R0}/(1-\delta_{R0})$, and RC/ABS also decreased significantly due to UV-B treatment. The decline in these components was found apparent especially in FR, TRC, and TRS populations (Fig. 2). Additionally, the UV-B injury index was calculated using PI_{ABS}. Populations were separated into three main groups according to injury level. The lowest index values were determined in TRS and FR populations (Group 3), whereas the highest index values were found in SP, RO, and TRI populations (Group 1) (Fig. 3).

UV-B radiation caused significant changes in the specific energy fluxes parameters (ABS/RC, TR_0/RC, ET_0/RC, DI_0/RC, and RE_0/RC), indicating differences in the behaviour/activities of photosystems of the tested populations (Fig. 4). Moreover, a significant increase in both antenna size of an active reaction centre (ABS/RC) and the flux of energy dissipation in processes other than trapping per reaction centre (DI_0/RC), especially in FR, England (UK), TRC, and TRS populations, were observed. Maximum trapped exciton flux per active reaction centre (TR_0/RC) and the flux of electrons transferred from Q_A^- to PQ per active reaction centre (ET_0/RC) also increased in

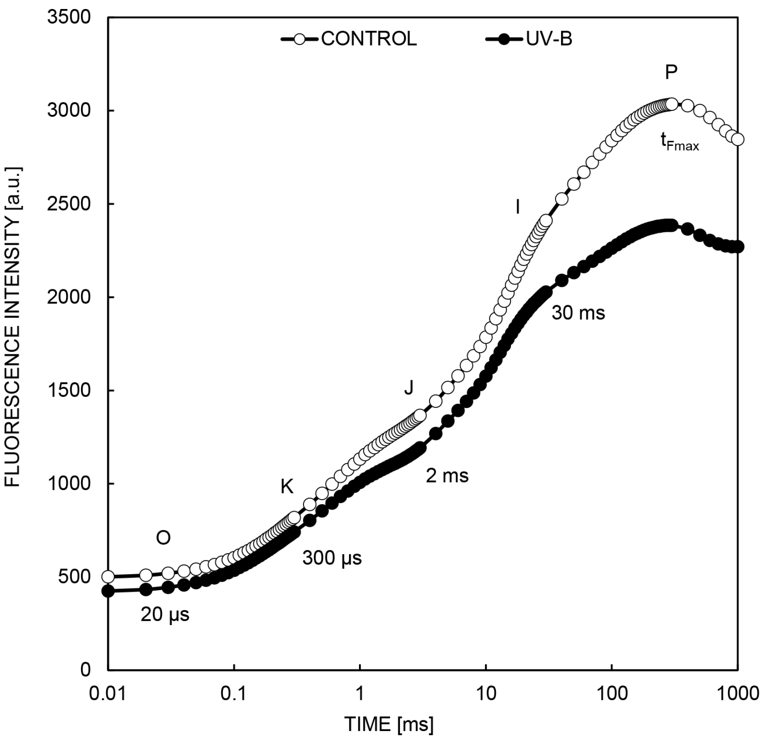

Fig. 1. A characteristic polyphasic chlorophyll *a* fluorescence rise OJIP, exhibited by examined Scots pines (*open* and *closed circle symbols* represent the average values of control and UV-B treated needles, respectively). To demonstrate the effect of UV-B radiation more clearly, the means of the control (kept at the controlled conditions and not exposed to UV-B) and treatment values of all populations were calculated and the graph was drawn using these values. The transient is plotted on a logarithmic time scale from 20 µs to 1 s.

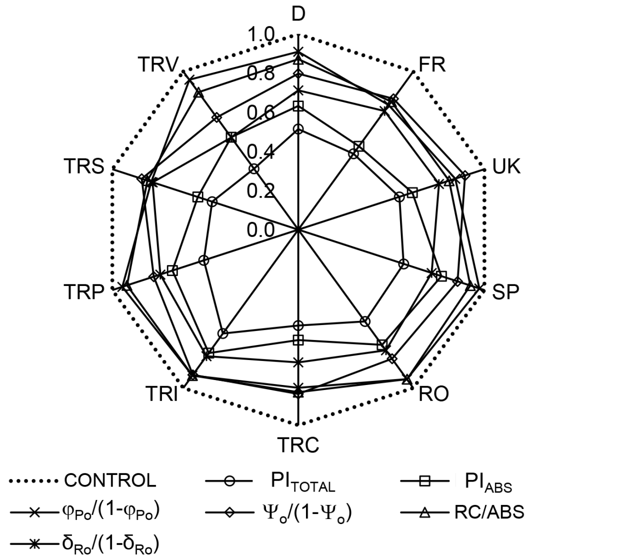

Fig. 2. Radar plot depicting the changes in photosynthetic total performance index (PI_{TOTAL}) and its components of Scots pine populations which were exposed to UV-B radiation. PI_{ABS} – the performance index for the photochemical activity; PI_{TOTAL} – total performance index; $\varphi_{P0}/(1 - \varphi_{P0})$ – indicator of the effectiveness of primary photochemical reaction; RC/ABS – Q_A reducing RCs per PSII antenna chlorophyll; $\Psi_0/(1 - \Psi_0)$ – the ratio of electrons removed from the system and electrons accumulated in the system; $\delta_{R0}/(1 - \delta_{R0})$ – quantum yield of reduction of end electron acceptors at the PSI. Country codes: D – Germany; FR – France; UK – England; SP – Spain; RO – Romania; TRC – Turkey, Çatacık; TRI – Turkey, Ilgaz; TRP – Turkey, Pınarbaşı; TRS – Turkey, Sarıkamış; TRV – Turkey, Vezirköprü).

all studied Scots pine populations, except in RO. On the other hand, the electron transport from Q_A^- to end electron acceptors at PSI acceptor side (RE_0/RC) significantly decreased in all of them (Fig. 4).

Some parameters related to the phenomenological energy fluxes through cross section of the sample (CS_0), such as absorbed energy (ABS/CS_0), trapped energy (TR_0/CS_0 and ET_0/CS_0), dissipated energy (DI_0/CS_0); and percentage of active reaction centres (RC/CS_0) displayed alterations due to UV-B radiation treatment, as compared to their controls. DI_0/CS_0 increased in TRC and TRS populations, while decreased in German (D), RO, and Kayseri-Pınarbaşı (TRP) populations, and it was close to their control values in other five populations (FR, UK, SP, TRI, and TRV). ABS/CS_0, TR_0/CS_0, ET_0/CS_0, and RC/CS_0 significantly declined by UV-B radiation in all populations. The highest decreases in these energy flux parameters were found in D population, while the lowest decreases were found in SP, TRI, and RO populations (Fig. 5).

UV-B radiation significantly affected donor side of PSII (V_K/V_J,), which points out to possible damage and inactivation of the oxygen-evolving complex (OEC). The highest increase was determined in FR, UK, and TRS populations, while the smallest was found in RO (Fig. 6). In contrast to V_K/V_J; Area, $SFI_{(abs)}$, and ΔV_{IP} parameters significantly decreased in all populations. Area, which is the area above OJIP fluorescence curve, significantly decreased in all studied populations, especially in German (D), FR, and TRS populations (about 40–50%). The decreases in structure–function indexes, $SFI_{(abs)}$, were found between about 10–30%, whereas the declines in the relative amplitude of the I–P phase of Chl *a* fluorescence (ΔV_{IP}) were approx. 16–40% (the lowest in TRI and the

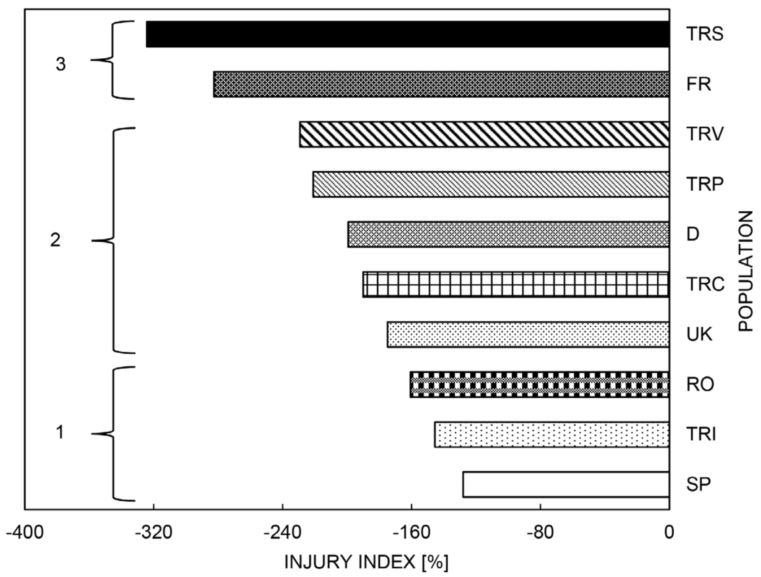

Fig. 3. The UV-B injury index of Scots pine populations. Damage index values were calculated by performance index (PI_{ABS}) according to Glerum (1985) modified equation ($PI_{UV\text{-}B}$ – $PI_{CONTROL}$)/(1 – [$PI_{CONTROL}$/100]) × 100. Country codes: D – Germany; FR – France; UK – England; SP – Spain; RO – Romania; TRC – Turkey, Çatacık; TRI – Turkey, Ilgaz; TRP – Turkey, Pınarbaşı; TRS – Turkey, Sarıkamış; TRV – Turkey, Vezirköprü).

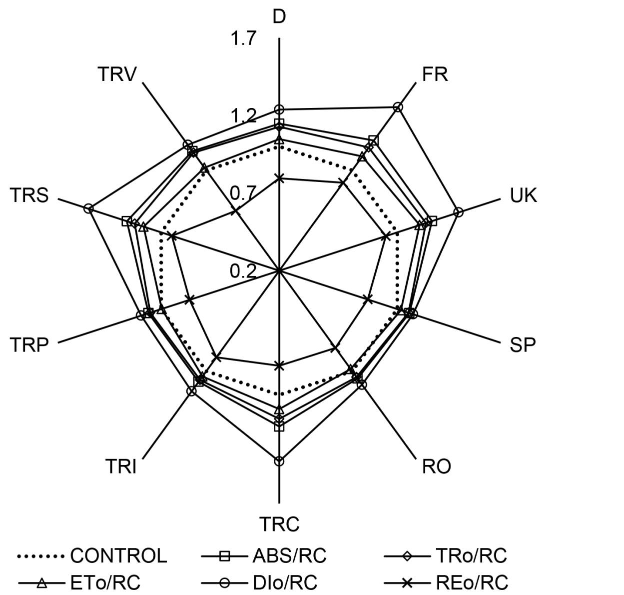

Fig. 4. The UV-B impact on specific energy fluxes of Scots pine populations. ABS/RC – absorption energy flux per active reaction center (apparent antenna size of an active PSII); DI_0/RC – total energy dissipated per reaction center; ET_0/RC – the electron flux transferred per active reaction center; RE_0/RC – the electron flux transferred per active reaction center and reducing terminal acceptors on the acceptor side of PSI; TR_0/RC – maximum trapped exciton flux per active reaction center. Country codes: D – Germany; FR – France; UK – England; SP – Spain; RO – Romania; TRC – Turkey, Çatacık; TRI – Turkey, Ilgaz; TRP – Turkey, Pınarbaşı; TRS – Turkey, Sarıkamış; TRV – Turkey, Vezirköprü).

highest in Vezirköprü TRV) (Fig. 6). As a general result, UV-B radiation led to a decrease in the photosynthetic efficiency and performance of Scots pine populations. FR, TRC, and TRS populations were found to be more susceptible to UV-B radiation than other populations. SP, RO, and TRI populations exhibited better photosynthetic performance in response to UV-B treatment.

The JIP-test parameters among genotypes of Scots pine populations that were captured by the first two PCA axes could explain 90% of the variation (Fig. 7). PCA 1 and 2 explained 77.5 and 13.3% of the variation in JIP-test, respectively. According to the hierarchical clustering of principal components showed that the best-supported number of cluster could be 4. PCA analysis revealed that specific fluxes (per RC), except RE_0/RC and V_K/V_J, had a positive contribution on first cluster which was reflecting the UV-B stress. Whereas, the other JIP-test parameters had a positive contribution on control groups. The results confirmed that the TRI-C and TRI-UV populations were very close reflecting the similar photosynthetic performance under UV-B applications (Fig. 7).

Discussion

Sunlight is an essential energy source to carry out the photosynthetic process in plants. However, UV-B, which is one of the components of sunlight, can harm photosynthetic apparatus. The downregulation of photosynthesis by UV-B radiation occurs due to the inhibition of the activities of the photosystems and CO_2 fixation enzymes (such as Rubisco), and the loss in integrity of the thylakoid membranes (Jordan *et al*. 1992, Teramura and Sullivan 1994, Vass 1997).

Chl *a* fluorescence is one of the commonly used methods to examine the photosystem efficiency and to screen the stress tolerance of plants (Murchie and Lawson 2013, Lazár 2015, Kalaji *et al*. 2016). The OJIP transient depicts the rate of reduction kinetics of various components of photosystems (Schansker *et al*. 2005, Duarte *et al*. 2017). The typical shape of OJIP transient curve which has three main phases including O–J, J–I, and I–P (Strasser *et al*. 1995) was influenced by UV-B in the present study (Fig. 1). I–P, the slowest phase of fluorescence, is associated with the gradual reduction of the residual electron transport chain, PSI acceptors, and entirely reduction of the PQ pool

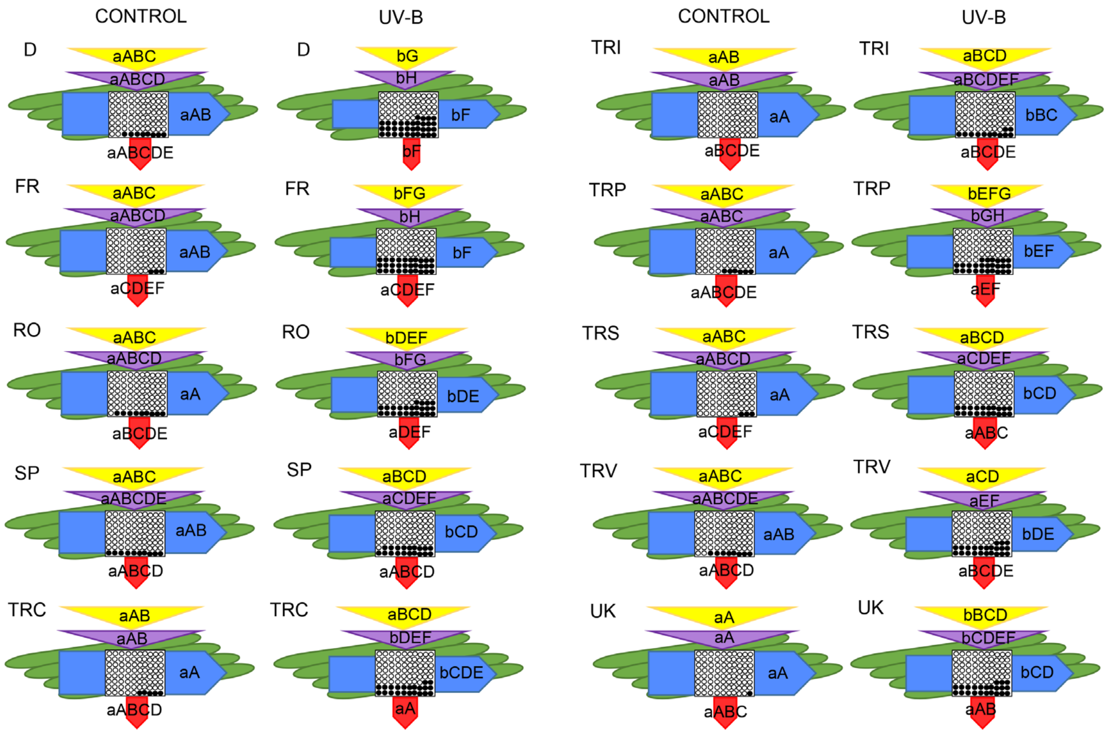

Fig. 5. The UV-B impact on phenomenological energy fluxes of Scots pine populations. Each relative value is drawn by the width of corresponding arrow, representing the mean value (n = 10) of a parameter. The value of absorbance (ABS/CS_0 – *yellow arrow*), trapping flux (TR/CS_0 – *purple arrow*), electron transport (ET/CS_0 – *blue arrow*) or heat dissipation of excess light (DI/CS_0 – *red arrow*), all expressed per leaf cross section (CS_0). *The black points* represent the fraction of inactive reaction centers. The different *small* and *capital letters* in each parameter arrow represent significant differences (P<0.05) between treatment of the same population and among populations, respectively. Country codes: D – Germany; FR – France; UK – England; SP – Spain; RO – Romania; TRC – Turkey, Çatacık; TRI – Turkey, Ilgaz; TRP – Turkey, Pınarbaşı; TRS – Turkey, Sarıkamış; TRV – Turkey, Vezirköprü).

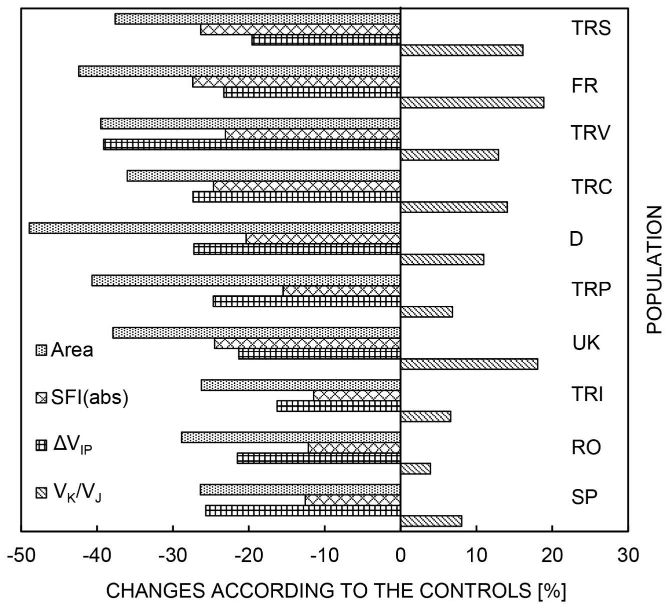

Fig. 6. Changes in selected JIP-test parameters assessing the behaviour of PSII in Scots pine populations exposed to UV-B radiation. Area – the area above the fluorescence induction curve (reflecting the size of the PQ pool); $SFI_{(abs)}$ – an indicator of PSII structure and functioning; ΔV_{IP} – a measure for the PSI content or PSII/PSI ratio of photosynthetic apparatus; V_K/V_J – inactivation and probable damage of the OEC. Country codes: D – Germany; FR – France; UK – England; SP – Spain; RO – Romania; TRC – Turkey, Çatacık; TRI – Turkey, Ilgaz; TRP – Turkey, Pınarbaşı; TRS – Turkey, Sarıkamış; TRV – Turkey, Vezirköprü).

(Schansker *et al*. 2006, Goltsev *et al*. 2016). This phase (I–P) was smaller in the UV-B treated seedlings compared to their controls (Fig. 1). It has been proved that ΔV_{IP}, the relative contribution of the I–P amplitude to the OJIP rise, is a measure for the PSI content or PSII/PSI ratio of photosynthetic apparatus (Ceppi *et al*. 2012, Çiçek *et al*. 2018). Results of the ΔV_{IP} of UV-B-treated populations are consistent with the response in I–P amplitude. The highest

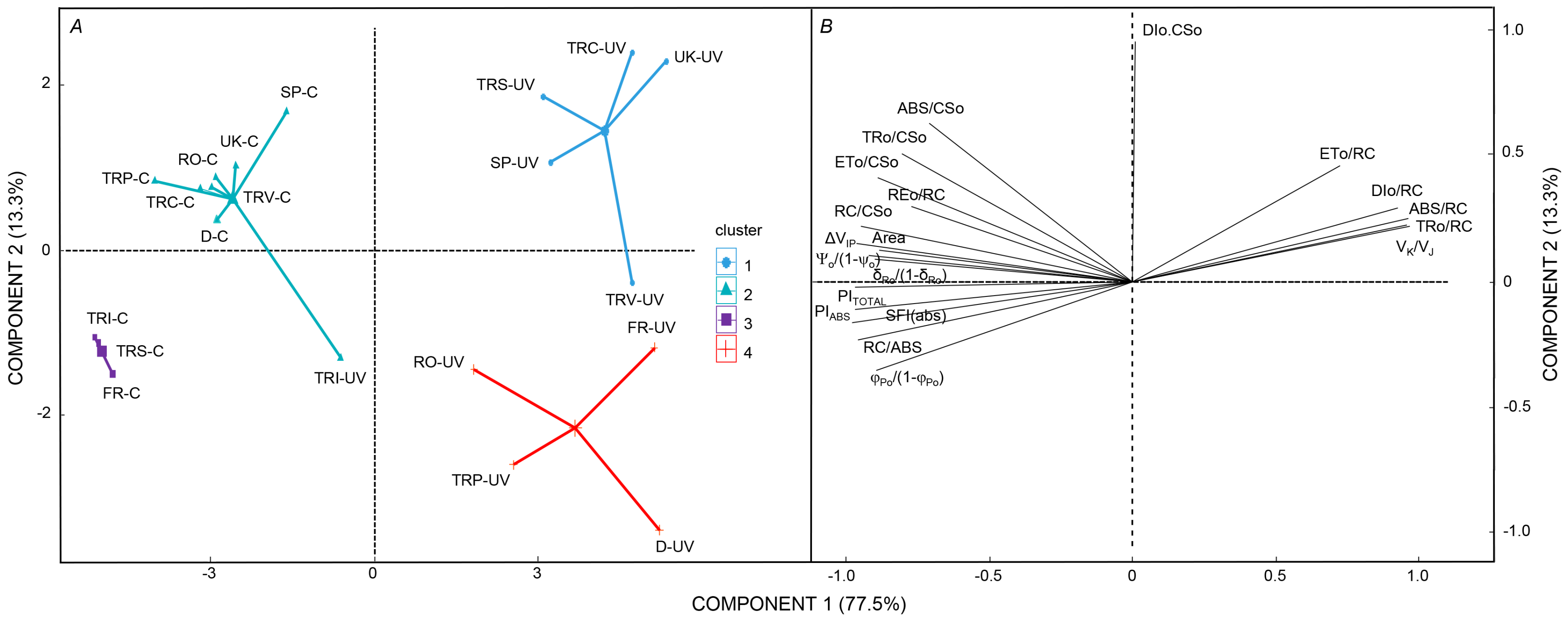

Fig. 7. Principal Component Analysis (PCA) of variability of JIP-test parameters in leaves of Scots pine populations exposed to UV-B radiation. (*A*) *k*-means clusters, (*B*) JIP-test parameters. Country codes: D – Germany; FR – France; UK – England; SP – Spain; RO – Romania; TRC – Turkey, Çatacık; TRI – Turkey, Ilgaz; TRP – Turkey, Pınarbaşı; TRS – Turkey, Sarıkamış; TRV – Turkey, Vezirköprü). Area – total complementary area between fluorescence induction curve and F_m; ABS/RC – absorption energy flux per active reaction center (apparent antenna size of an active PSII); DI_0/RC – total energy dissipated per reaction center; ET_0/RC – the electron flux transferred per active reaction center; RE_0/RC – the electron flux transferred per active reaction center and reducing terminal acceptors on the acceptor side of PSI; TR_0/RC – maximum trapped exciton flux per active reaction center; V_K/V_J – limitation/inactivation and possibly damage of the oxygen-evolving complex; PI_{TOTAL} – total performance index; PI_{ABS} – the performance index for the photochemical activity; $\varphi_{P0}/(1-\varphi_{P0})$ – indicator of the effectiveness of primary photochemical reaction; RC/ABS – Q_A reducing RCs per PSII antenna chlorophyll; $\Psi_0/(1-\Psi_0)$ – the ratio of electrons removed from the system and electrons accumulated in the system; $\delta_{R0}/(1-\delta_{R0})$ – quantum yield of reduction of end electron acceptors at the PSI; ABS/CS_0 – absorbed photon flux per CS_0; TR_0/CS_0 – maximum trapped exciton flux per CS_0; ET_0/CS_0 – the flux of electrons from Q_A^- to PQ per CS_0; RC/CS_0 – amount of active PSII RCs per CS_0; DI_0/CS_0 – thermal dissipation of energy in PSII per CS_0; ΔV_{IP} – amplitude of the relative variable fluorescence of the I to P rise; $SFI_{(abs)}$ – an indicator of PSII 'structure and functioning'.

decrease in ΔV_{IP} was observed in TRS by 40%, whereas the lowest decrease was found in TRI by 16% (Fig. 6). These results indicated to that UV-B radiation decreased the PSI content of Scots pines. Previous studies confirm that I–P phase and ΔV_{IP} are sensitive to various environmental stresses (Oukarroum *et al*. 2009, Ceppi *et al*. 2012, Çiçek *et al*. 2018). Meanwhile, many studies reported that PSII is more sensitive to UV-B (Kulandaivelu and Noorudeen 1983, Takahashi *et al*. 2010), because oxygen-evolving complex, D1, and D2 proteins in PSII are the most affected by UV-B due to their chemical structures (Vass 1997, Jansen *et al*. 1998, Kataria *et al*. 2014, Faseela and Puthur 2018). But, UV-B treatment unfavourably influenced both acceptor and donor sides of the photosystems in the present study.

The populations were separated into three groups according to the injury index calculated utilizing PI_{ABS} (Fig. 3). Group 3 involved TRS and FR populations, which revealed low photosynthetic activity, whereas Group 1 includes SP, RO, and TRI populations, which showed high photosynthetic activity. Specific energy fluxes (ABS/RC, TR_0/RC, ET_0/RC, and DI_0/RC, except RE_0/RC) of all three groups increased under UV-B treatment as compared to controls, while RE_0/RC of all populations decreased by different levels (Fig. 4). At the same time, dissipated energy (DI_0/RC) was found the highest in FR and TRS populations, *i.e.*, these populations had to dissipate the excitation energy as heat and fluorescence more than photochemical quenching as 'cost of survival'. In addition, it was observed that the decrease in RE_0/RC was in parallel with the response of ΔV_{IP}. These parameters are relatively associated with PSI functionality. The reduction in RE_0/RC was correlated with the increase in DI_0/RC, suggesting that UV-B treatment induced the dissipation of damaging excess energy. Phenomenological energy fluxes (ET_0/CS_0, TR_0/CS_0, ABS/CS_0, and RC/CS_0, except DI_0/CS_0) of all examined populations decreased in comparison to their controls (Fig. 5). DI_0/CS_0 increased in TRC and TRS by 10 and 16%, whereas it significantly decreased in TRP and D by about 17 and 22%, respectively. These results are in agreement with findings of the previous studies of plants exposed to various stresses (Çiçek *et al*. 2012, Sitko *et al*. 2017, Kalaji *et al*. 2018).

UV-B radiation adversely affected donor side of the PSII, $SFI_{(abs)}$ and Area (Fig. 6). The inactivation of the OEC, V_K/V_J, increased in all population [especially in FR, TRS (Group 3), UK and TRC (Group 2)] by about 13–19%. The increase in V_K/V_J may mean that there is a possible damage in the OEC. It might be suggested that populations of Group 1 achieved to maintain the donor side of PSII, because of their lesser increase in the V_K/V_J ratio. $SFI_{(abs)}$ and Area decreased with UV-B approximately by 27 and 50%, respectively. The difference between the lowest decrease of Area in Group 1 and other two groups was about 40%, this difference is approx. 36% for $SFI_{(abs)}$. Strasser *et al*. (2000) have notified that the declines in Area occur due to the inhibition of electron transport from reaction centres to the plastoquinone pool during stress.

UV-B treatment negatively affected the vitality indexes (PI_{TOTAL} and PI_{ABS}) and their components (absorption, trapping, conversion into the electron transport of energy). The largest decrease in PI_{TOTAL} and PI_{ABS} were found in FR and TRS populations of Group 3 (by about 45%), whereas the least declines were found in the population of Group 1 (by approx. 25%) (Fig. 2). The declines of all populations were related to downregulation of electron transport. Photosynthetic performance (vitality) indexes and injury degree of populations allowed classification of the populations to three UV-B tolerance levels: UV-B tolerant (Group 1; SP, RO, and TRI); moderately UV-B tolerant (Group 2; D, UK, TRC, TRP, and TRV); and UV-B sensitive (Group 3; FR, TRS).

Scots pine populations exhibited differences in responses to UV-B due to probably their genetic capacity and protective mechanisms. FR and TRS populations were significantly affected by UV-B radiation more than others, whereas SP and TRI populations showed better photosynthetic capacities. Excitation energy was dissipated as heat and fluorescence (high DI_0/RC and DI_0/CS_0) in FR and TRS populations, so absorbed energy could not be directed to photosystems for photochemistry. Populations derived from different regions of Europe and Anatolia might have been adapted to a wide range of environmental and geographical conditions, thus acquiring a tolerant character within this period and yielding different responses to UV-B radiation. Wang *et al*. (2016) have stated that plant populations from high and low elevations may differ in acclimation to changes in UV radiation. SP, RO and, TRI, which were UV-B-tolerant populations according to photochemical performance, might probably have colonized from the same origin (or refugia) in their phylogenetic history. Moreover, it has been suggested that current populations of Scots pine in Europe originate from at least three different glacial refuges (Sinclair *et al*. 1999). Therefore, further studies based on molecular data are needed to explain the evolutionary history of these Scots pine populations.

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Appendix. Equations and descriptions for calculation of selected JIP-test parameters (Strasser *et al*. 2010, Goltsev *et al*. 2016, Ripoll *et al*. 2016, Stirbet *et al*. 2018).

Fluorescence parameters	Description
F_0	Initial fluorescence intensity, when all PSII RCs are open
F_{300}	Fluorescence intensity at 300 μs
F_J	Fluorescence intensity at the J-step (at 2 ms)
F_I	Fluorescence intensity at the I-step (at 30 ms)
F_m	Maximal fluorescence intensity, when all PSII RCs are closed
V_J	$(F_{2ms} – F_0)/(F_m – F_0)$, relative variable fluorescence at the J-step (2 ms)

V_I	$(F_{30ms} – F_0)/(F_m – F_0)$, relative variable fluorescence at the I-step (30 ms)
V_K	$(F_{300µs} – F_0)/(F_m – F_0)$, relative variable fluorescence at the K-step (300 µs)
M_0 or (dV/dt)o	$4(F_{300µs} – F_0)/(F_m – F_0)$, initial slope (in ms^{-1}) of the O–J fluorescence rise
Area	Total complementary area between fluorescence induction curve and F_m
V_K/V_J	Limitation/inactivation and possibly damage of the oxygen-evolving complex
$φ_{P0} = TR_0/ABS$	F_v/F_m, maximum quantum yield of PSII photochemistry
$φ_{E0} = ET_0/ABS$	$φ_{P0} × Ψ_0$, quantum yield for electron transport from $Q_A^–$ to PQ
o = ET_0/TR_0	$1 – V_J$, efficiency with which a PSII trapped electron is transferred from $Q_A^–$ to PQ
$φ_{D0} = 1 – φ_{Po}$	F_0/F_m, the quantum efficiency of energy dissipation
$δ_{R0} = RE/ET_0$	$(1 – V_I)/(1 – V_J)$, the efficiency with which an electron from PQH_2 is transferred to final PSI acceptors
$φ_{R0} = RE_0/ABS$	$φ_{P0o} × Ψ_0 × δ_{R0}$, the quantum yield of electron transport from $Q_A^–$ to the PSI end electron acceptors
RC/ABS	Q_A reducing RCs per PSII antenna chlorophyll (reciprocal of ABS/RC)
ABS/RC	$(M_0/V_J)/φ_{Po}$, specific absorption flux per RC (apparent antenna size of an active PSII)
TR_0/RC	M_0/V_J, maximum trapped exciton flux per RC
ET_0/RC	$(M_0/V_J) × Ψ_0$, the flux of electrons transferred from $Q_A^–$ to PQ per RC
RE_0/RC	the electron flux transferred from $Q_A^–$ to final PSI acceptors per RC
DI_0/RC	$ABS/RC – TR_0/RC$, the flux of energy dissipated in processes other than trapping per RC
ABS/CS_0	Absorbed photon flux per CS
TR_0/CS_0	$(TR_0/ABS) × (ABS/CS_0)$, maximum trapped exciton flux per CS
ET_0/CS_0	$(ET_0/ABS) × (ABS/CS_0)$, the flux of electrons from $Q_A^–$ to PQ per CS
RC/CS_0	$φ_{P0} × (V_J/M_0) × F_0$, amount of active PSII RCs per CS
DI_0/CS_0	$(ABS/CS_0) – (TR_0/CS_0)$, thermal dissipation of energy in PSII per CS
V_{IP}	$(F_P – F_I)/(F_P – F_0)$, amplitude of the relative variable fluorescence of the I to P rise
$SFI_{(abs)}$	$(RC/ABS) × φ_{P0} × Ψ_0$, an indicator of PSII ‘structure and functioning’
PI_{ABS}	$(RC/ABS) × φ_{P0}/(1 – φ_{P0}) × Ψ_0/(1 – Ψ_0)$, performance index on absorption basis related to the overall photosynthetic activity of PSII
PI_{TOTAL}	$(RC/ABS) × φ_{P0}/(1 – φ_{P0}) × Ψ_0/(1 – Ψ_0) × δ_{R0}/(1 – δ_{R0})$, performance index (potential) for energy conservation from photons absorbed by PSII to the reduction of PSI end acceptors